

Morphological Diversity of Anatomical Strepsirrhinism and the Evolution of the Lemuriform Toothcomb

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ABSTRACT The hypothesis that the vomeronasal organ has an important functional relationship with, and led to the evolution of, the prosimian toothcomb has not been well tested. This paper examines the diversity of anatomical strepsirrhinism across several mammalian taxa to determine if fossil and living strepsirrhine primates exhibit any derived characters that may highlight the functional link between the vomeronasal organ and the toothcomb, and to examine the potential importance of anatomical strepsirrhinism to toothcomb origins. Results indicate that extant gregarious lemuriforms are derived in having a relatively wide interincisal gap, providing an unobstructed line of communication between the vomeronasal organ and anterior rostral structures such as the toothcomb. This finding is consistent with the proposal that anatomical strepsirrhinism is functionally related to use of the toothcomb in grooming. However, the importance of the vomeronasal organ to toothcomb origins is less clear. If the morphology of adapiforms and non-gregarious lemuriforms is representative of the morphology of basal lemuriforms, then it can be inferred that early lemuriforms did not possess the wide-gap autapomorphy; hence, anatomical evidence discussed here cannot be used to rule out non-social hypotheses of toothcomb origins. *Am J Phys Anthropol* 105:355–367, 1998. © 1998 Wiley-Liss, Inc.

The classification of primates into the suborders Haplorhini and Strepsirhini (Pocock, 1918) is nominally based on the morphology of the nasal region. The word “strepsirrhine” literally refers to the “twisted” appearance of the external nares (Hofer, 1976; I follow Jenkins, 1987, for spelling of “strepsirrhine” and lemuriform familial names). However, as used by most workers (e.g., Maier, 1991), anatomical strepsirrhinism indicates the continuity of the upper lip with the vomeronasal organ (also known as Jacobson’s organ; see Fig. 1).

The morphology of the anterior rostrum in strepsirrhine primates led Rosenberger and Strasser (1985) to propose a functional link between the vomeronasal organ and the toothcomb of lemuriform primates. Based on research that supports the role of the vomero-

nasal organ in sociosexual communication (Estes, 1972; Verberne, 1976), and on the connection between the rhinarium and vomeronasal organ via the gap between the central upper incisors (Hofer, 1977), these researchers hypothesized that the lemuriform toothcomb evolved as a sensory extension of the vomeronasal organ, serving as a tool for pheromone collection.

Rosenberger and Strasser (1985) further argued that the upper anterior dentition of Eocene adapid primates closely resembles that of modern lemuriforms and would have permitted the same continuity between the upper lip and vomeronasal organ. Hence,

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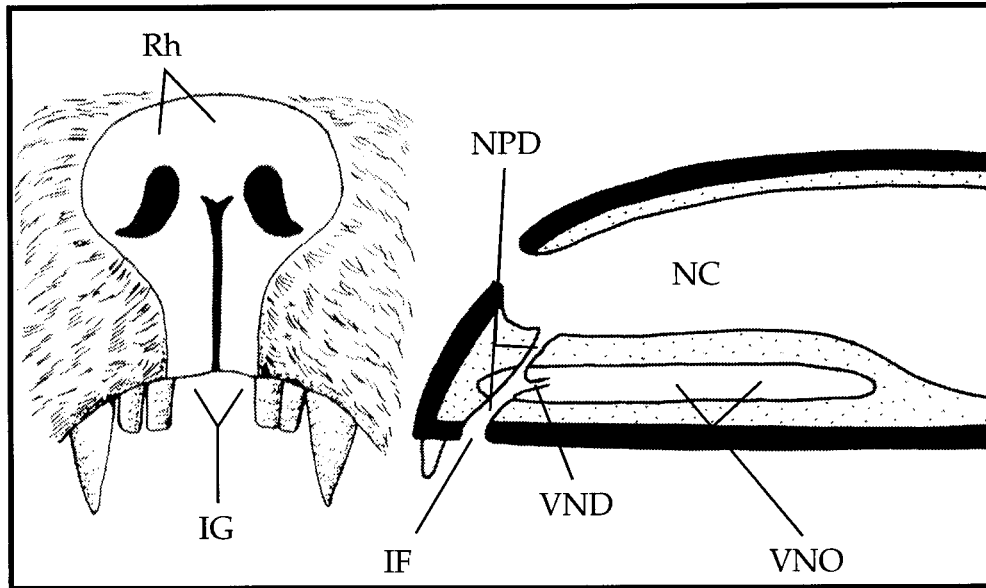


Fig. 1. Diagrammatic morphology of the anterior rostrum in a generalized, anatomically strepsirrhine primate (adapted from Martin, 1990). Abbreviations for all figures are as follows: CL = cleft lip; CT = connective tissue; IF = incisive foramen; IG = interincisal gap; NC = nasal cavity; NPD = nasopalatine duct; PM = premaxilla; PP = palatine papilla; Rh = rhinarium; VND = vomeronasal duct; VNO = vomeronasal organ; I(1, 2, 3) = upper incisors.

they considered Eocene adapids—which cannot be said to have any lower dental structure resembling a toothcomb—to have in their upper dentition a morphology “preadaptive” to the evolution of the toothcomb.

The process of grooming with the toothcomb must often result in stimulation of the vomeronasal organ . . . and similar sequences would probably have been present among adapids having a similar organization of the tissues of the snout. . . . [The] occurrence of a tethered sulcate philtrum in early strepsirrhine adapids . . . would be a preadaptation to the evolution of accessory organs [i.e., a toothcomb] which enhance its selective value, perhaps by more efficiently collecting and distributing pheromones (Rosenberger and Strasser, 1985:80).

This hypothesis on toothcomb origins is consistent with previous versions of the “grooming hypothesis” (e.g., Buettner-Janusch and Andrew, 1962; Szalay and Seligsohn, 1977) in which conspecific grooming is argued to be the most important selective pressure responsible for the form of the modern lemuriform toothcomb.

Criticism of Rosenberger and Strasser’s hypothesis by Beard (1988) focused on the assertion that adapiforms and lemuriforms share derived characters of the rostrum. As

discussed in a series of papers (Rosenberger and Szalay, 1980; Rosenberger et al., 1985; Rosenberger and Strasser, 1985), these characters of the central upper incisors included lack of apical interstitial contact, low crown height, the presence of mesially projecting prongs, and their occlusal pattern with the lower anterior tooththrow. Beard (1988) objected to just one of these: the purported lack of contact between the apices of the central upper incisors in *Notharctus*. (For additional criticism see Krishtalka et al., 1990, and Rasmussen, 1986.) More importantly, Beard noted that lemuriforms and adapiforms are not unique among mammals in possessing some sort of interincisal gap, citing its presence in scandentians, lipotyphlans, and various Early Tertiary fossils. Assuming that the interincisal gap was a consistent indicator of anatomical strepsirrhinism, he thus argued that strepsirrhinism is primitive for primates, and was probably not functionally associated with the apomorphic lemuriform toothcomb.

Although this critique made important points regarding rostral morphology in fossil

primates, Beard's response to Rosenberger and Strasser (1985) did not adequately examine their proposal that the vomeronasal organ is relevant to the function of the toothcomb. Beard (1988) asserted that the possession of a space between the central upper incisors in various eutherian orders indicates that the rostrum in lemuriforms is plesiomorphic. However, in addition to supporting the point that many groups of mammals have some kind of gap between their central upper incisors, the data collected—but not quantified—by Beard (1988) on relative gap size in various eutherians also show considerable differences among those that are anatomically strepsirrhine. These differences, and their potential relevance for Rosenberger and Strasser's theory of toothcomb evolution, have yet to be explored.

It is therefore my intent in this paper to reexamine Rosenberger and Strasser's proposal that the vomeronasal organ in primates is relevant to the function and evolution of the toothcomb. In order to accomplish this, I will ask two questions related to the polarity of the rostrum in toothcomb prosimians: 1) is anatomical strepsirrhinism homogeneous in primates and other mammals; and 2) are there data supporting Rosenberger and Strasser's proposal that the rostrum in lemuriforms and adapiforms is autapomorphic? If the answers to these questions are, respectively, yes and no, then Beard's (1988) criticism of Rosenberger and Strasser's hypothesis is justified. Otherwise, their proposal may be relevant to toothcomb evolution at some level.

MATERIALS AND METHODS

In order to assess the first question listed above, the palatal region of *Eulemur fulvus* (Primates), *Tupaia minor* (Scandentia), *Blarina brevicauda* (Lipotyphla), *Felis catus* (Carnivora), and *Ovis aries* (Artiodactyla) was dissected and dry skulls of genera in all of the preceding ordinal taxa were examined. Histologically prepared cross sections of *Blarina* were also used to document rostral morphology in that taxon. Soft-tissue specimens examined in this study were obtained from the Division of Laboratory Animal Resources (DLAR) and Anatomical Sciences (USBA) at the State University of

New York, Stony Brook, except for a specimen of *Tupaia minor*, which is in the collections of the Department of Mammalogy, American Museum of Natural History (AMNH), New York.

In order to address the second question listed above, I focused on the means by which the vomeronasal organ communicates with the external environment in primates, i.e., the upper interincisal gap (Hofer, 1977). In outlining their hypothesis, Rosenberger and Strasser (1985) emphasized that the gap between the upper incisors allows for effective communication between the toothcomb and vomeronasal organ. Thus, if Rosenberger and Strasser's proposed association between grooming and the vomeronasal organ is correct, then one might predict that lemuriforms that use the toothcomb most often for grooming would have a relatively wider channel between their central upper incisors than other mammals. That is, if one assumes that gregarious lemuriforms (e.g., *Eulemur*), due to their complex social structure and relatively frequent contact with conspecifics (Richard, 1987), allogroom more frequently than non-gregarious mammals (e.g., *Loris*), then one would expect the gregarious forms to possess a wider interincisal gap than other mammals.

To test these predictions, I measured the raw interincisal gap (i.e., the shortest distance in millimeters between the alveoli of the central upper incisors) across strepsirrhine mammals listed in Table 1. This measurement was scaled using two indices: the width of the palate at M1 (i.e., the shortest distance in millimeters between the lateral margins of the mesiobuccal cusps of the two upper M1s), and the estimated area of the first upper molar (i.e., the product of maximum mesiodistal and buccolingual dimensions). Raw measurements for all individual specimens are reported in Table 1. Measurements for extant taxa were obtained from crania housed in the Departments of Mammalogy at the AMNH and the Museum of Comparative Zoology (MCZ), Harvard University. Measurements for fossil taxa were obtained from casts in the USBA collection and from Beard (1988). Statistical comparisons were facilitated using the JMP statistical program for the Macintosh (Sall et al.,

TABLE 1. Data collected

Taxon	Museum no. ¹	Society ²	Palatal width (mm)	Interincisal gap (mm)	M1 area (mm)
Indri	100503	gregar	33.8	6.9	54.6
Indri	100507	gregar	34	6.7	54.0
Indri	100505	gregar	35.2	7.1	70.6
Indri	100506	gregar	33.3	7.3	66.4
Indri	185638	gregar	33.2	6.3	54.5
Indri	100816	gregar	34.8	7.2	61.6
Propithecus	100544	gregar	27.2	3.3	44.0
Propithecus	100552	gregar	25.7	3.3	40.6
Propithecus	100540	gregar	26	3.2	45.4
Propithecus	100545	gregar	26.9	3.3	42.7
Propithecus	100548	gregar	25.7	3.3	47.4
Propithecus	100557	gregar	30	3.7	51.1
Propithecus	100556	gregar	28.5	4	46.2
Avahi	100635	gregar	17.3	3.3	17.6
Avahi	100461	gregar	16.8	4.6	17.6
Avahi	41267	gregar	16.5	3.8	15.5
Avahi	170494	gregar	17.9	4.4	16.0
Avahi	MCZ44878	gregar	19.2	4.2	18.9
Avahi	MCZ44879	gregar	18.3	4.3	18.1
Varecia	35561	gregar	33.1	4.5	53.1
Varecia	77828	gregar	33.8	4.8	60.1
Varecia	70220	gregar	34	4.1	60.8
Varecia	35109	gregar	30.1	4.4	52.5
Varecia	35090	gregar	32.8	4.5	64.0
Varecia	100510	gregar	34	5.5	59.2
Varecia	100511	gregar	28.8	5.7	48.8
Hapalemur	100534	gregar	18.7	3.8	21.0
Hapalemur	100535	gregar	18.9	3.9	19.3
Hapalemur	100628	gregar	19.8	3.4	22.8
Hapalemur	100536	gregar	20.4	4.5	22.8
Hapalemur	100823	gregar	18.5	4.2	20.6
Hapalemur	170682	gregar	20.1	4.1	24.8
Hapalemur	170693	gregar	20.8	4.7	23.4
Eulemur	100819	gregar	27.2	7.6	47.2
Eulemur	100522	gregar	24.2	6.8	30.1
Eulemur	100532	gregar	26	6.4	41.0
Eulemur	100523	gregar	25.4	6.7	40.3
Eulemur	100538	gregar	23.9	5.7	28.9
Eulemur	100520	gregar	23.8	5.3	29.4
Eulemur	100610	gregar	23.3	5.2	30.6
Eulemur	100609	gregar	24.6	5.6	25.0
Lemur	170741	gregar	22.3	4.5	27.9
Lemur	170737	gregar	23.8	4.8	26.9
Lemur	170743	gregar	22.6	3.9	24.3
Lemur	170744	gregar	23.9	5.2	25.2
Lemur	100824	gregar	23.7	5.1	26.8
Lemur	100821	gregar	23.5	4.3	29.6
Phaner	100829	gregar	14.3	2.8	7.0
Phaner	285	gregar	14	2.9	7.6
Phaner	MCZ44954	gregar	15	2.6	8.1
Phaner	MCZ44953	gregar	14.6	2.6	7.8
Euoticus	241127	semi-gr	13.8	3.6	10.1
Euoticus	114203	semi-gr	13.1	3.4	9.1
Euoticus	236352	semi-gr	13	3.8	8.2
Euoticus	236350	semi-gr	12.6	3.7	9.5
Euoticus	241126	semi-gr	13.1	3.7	9.2
Euoticus	119863	semi-gr	12.6	3	8.8
Euoticus	119803	semi-gr	12.3	3.1	8.2
Otolemur	149693	semi-gr	22.9	3.1	21.7
Otolemur	80238	semi-gr	22.1	2.7	20.0
Otolemur	187364	semi-gr	18.9	2.8	19.9
Otolemur	114155	semi-gr	21.1	3	20.3
Otolemur	88064	semi-gr	22.8	3.4	21.9
Otolemur	88063	semi-gr	22.5	3.2	19.9
Otolemur	88062	semi-gr	22.8	3.5	20.5
Galago	187356	semi-gr	12.5	1.8	8.6
Galago	187359	semi-gr	12.7	2	9.1
Galago	187367	semi-gr	14.2	2.3	8.8

TABLE 1. (continued)

Taxon	Museum no. ¹	Society ²	Palatal width (mm)	Interincisal gap (mm)	M1 area (mm)
Galago	187360	semi-gr	11.8	1.6	7.9
Galago	187355	semi-gr	12.4	1.7	7.7
Galago	187358	semi-gr	12.8	1.8	7.9
Galago	187357	semi-gr	12.7	2.1	8.5
Galago	187361	semi-gr	12.7	1.8	8.2
Microcebus	174464	semi-gr	8.3	1	3.2
Microcebus	174455	semi-gr	8.8	1	3.7
Microcebus	174449	semi-gr	8.6	0.9	3.4
Microcebus	174463	semi-gr	8.2	1.1	3.0
Microcebus	174462	semi-gr	8.7	1	3.3
Microcebus	174465	semi-gr	8.3	1	3.0
Microcebus	174461	semi-gr	8.3	0.9	2.8
Microcebus	174466	semi-gr	8.4	1	3.3
Arctocebus	212576	non-gr	17	2.4	15.9
Arctocebus	212954	non-gr	15.8	2	15.4
Arctocebus	207949	non-gr	15.2	2.4	14.6
Nycticebus	87279	non-gr	19.6	2	20.1
Nycticebus	60766	non-gr	18.8	1.9	17.6
Nycticebus	165656	non-gr	21.2	2.1	19.7
Nycticebus	112991	non-gr	21.4	2.3	19.7
Nycticebus	240010	non-gr	20.8	2	20.9
Nycticebus	164442	non-gr	21.1	2.3	19.1
Loris	22718	non-gr	14.7	1.6	9.3
Loris	150059	non-gr	11.8	0.9	9.6
Loris	34257	non-gr	11.5	1.7	9.0
Loris	34256	non-gr	12.4	1.2	8.1
Loris	150062	non-gr	11.8	1.2	10.7
Loris	165931	non-gr	14.3	1.7	11.0
Loris	165930	non-gr	14.6	2	12.3
Cheirogaleus	100640	semi-gr	17.1	2.5	11.8
Cheirogaleus	80072	semi-gr	17.1	2.2	13.1
Cheirogaleus	100652	semi-gr	12.4	1.5	5.9
Cheirogaleus	MCZ44946	semi-gr	18.7	2.6	13.6
Cheirogaleus	MCZ44952	semi-gr	17	2.5	9.6
Cheirogaleus	MCZ44948	semi-gr	20.4	3	16.4
Cheirogaleus	MCZ44949	semi-gr	19.2	2.8	13.6
Perodicticus	119865	non-gr	21.1	1.8	16.3
Perodicticus	119869	non-gr	22.8	2.5	17.5
Perodicticus	119868	non-gr	23.7	2.4	18.6
Perodicticus	241117	non-gr	19.5	2.4	14.3
Perodicticus	54340	non-gr	22.4	2	16.6
Tupaia	101663	non-gr	11.8	1.6	8.9
Tupaia	101664	non-gr	12.1	1.7	8.9
Tupaia	101665	non-gr	12.3	1.6	7.8
Tupaia	101667	non-gr	12.7	1.8	8.4
Tupaia	101668	non-gr	12.1	1.9	7.3
Tupaia	101669	non-gr	12	1.7	7.3
Tupaia	101670	non-gr	12.3	1.8	7.3
Tupaia	101671	non-gr	12	1.8	8.1
Tupaia	101672	non-gr	12.2	2	8.1
Tupaia	101673	non-gr	12	2	6.5
Tupaia	101674	non-gr	12.2	1.7	6.7
Setifer	170548	non-gr	17.5	1.8	13.8
Setifer	170583	non-gr	14.4	1.4	10.7
Setifer	100749	non-gr	19.5	1.9	19.7
Setifer	100762	non-gr	16.1	1.4	14.8
Setifer	170581	non-gr	17.1	1.6	11.0
Setifer	170550	non-gr	13.9	1.5	12.0
Setifer	100750	non-gr	16.1	2	15.9
Smilodectes	Beard '88	?	—	2.4	30.6
Notharctus	Beard '88	?	—	2.2	29.4
Notharctus	Beard '88	?	—	2.75	32.8
Leptadapis	USBA ad1	?	31.1	3.5	54.8
Adapis	USBA m7	?	21.1	2.2	21.6
Adapis	USBA m4	?	20.9	2.9	19.3

¹ Unless indicated otherwise, all museum numbers refer to collections at the AMNH.² "Gregar" = gregarious; "semi-gr" = semi-gregarious; "non-gr" = non-gregarious.

1994). Unless stated otherwise, statements of statistical difference are based on the nonparametric Kruskal-Wallis test (see Sokal and Rohlf, 1995).

Generalizations about social behavior in groups of mammals are difficult to make. Nevertheless, for the purposes of the present study three different categories were recognized: First, taxa that habitually spend active time in the presence of one or more conspecifics were designated "gregarious;" this category includes lemurids and indrids (Richard, 1987), plus the cheirogaleid *Phaner* (Charles-Dominique, 1978). Second, taxa that often forage alone but typically form sleeping groups containing multiple adults were designated "semi-gregarious;" this category includes galagonids, *Cheirogaleus*, and *Microcebus* (Bearder, 1987; Charles-Dominique, 1977). Third, taxa that forage alone and do not typically form sleeping groups containing more than mother and offspring were designated "non-gregarious;" this category includes lorids, *Tupaia*, and *Setifer* (Bearder, 1987; Charles-Dominique, 1977; Eisenberg and Gould, 1970; Nowak, 1991).

RESULTS

Is anatomical strepsirrhinism homogeneous across mammals?

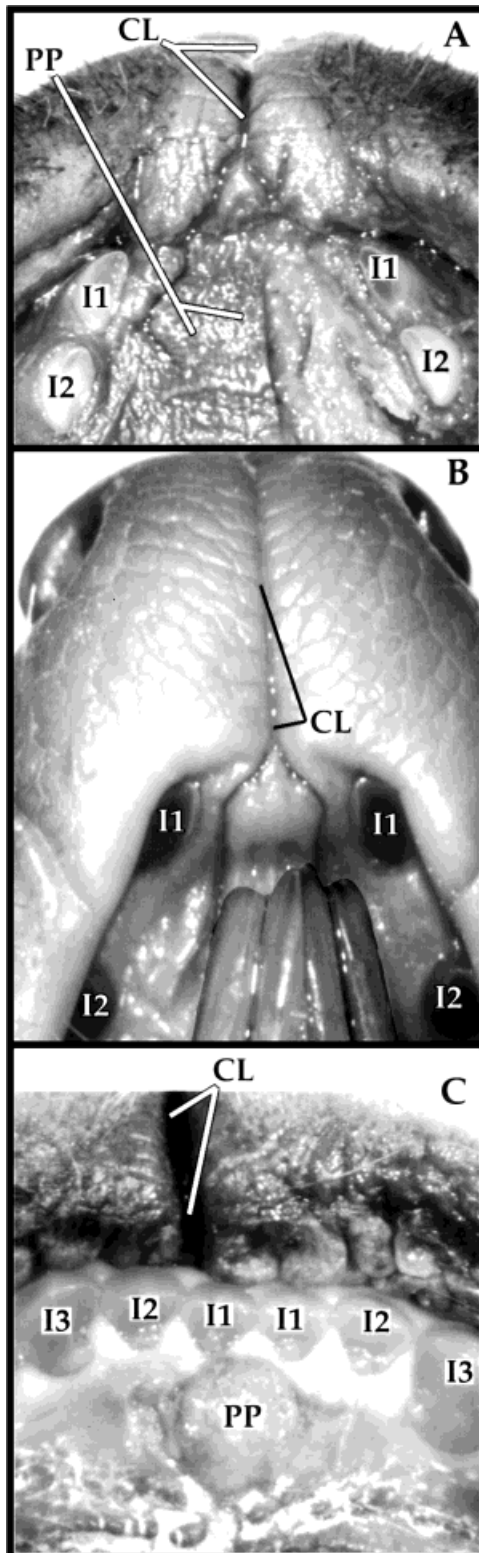
In *Eulemur fulvus* and *Tupaia minor*, the path between the nasopalatine ducts and upper lip is folded to provide greater surface area, permitting material to flow freely between the oral cavity and cleft upper lip (Figs. 2A, 2B). In both taxa, the upper interincisal gap clearly facilitates the connection between the vomeronasal organ and rhinarium. *Microcebus murinus* has a similar morphology (Schilling, 1970); in this taxon, the anterior lumina of the paired vomeronasal organ are connected to the nasopalatine canals via short vomeronasal ducts. The nasopalatine canals, in turn, connect the nasal and oral cavities, ventrally opening up into ducts on either side of the palatine papilla. In cross section, the palatine papilla is an inverted mushroom-shaped structure (Schilling, 1970) that allows *Eulemur*, *Microcebus*, and *Tupaia* a means of closing the nasopalatine canals by pressing up against the papilla with the tongue. A stereotyped behavior involving the

tongue and lip (known as "flehmen") observed in *Lemur catta* probably augments the transport of substances from the anterior rostrum to the vomeronasal organ (Bailey, 1978).

The domestic cat has a cleft upper lip, moist rhinarium, patent nasopalatine canals, palatine papilla (Fig. 2C) and a well-developed vomeronasal organ (Verberne, 1976). By virtue of these characters, it is strepsirrhine. Nevertheless, cats have a tightly packed row of incisors, allowing for no gaps within the upper anterior toothrow. Examination of dry skulls of canid, mustelid, procyonid, ursid, viverrid, and other carnivoran taxa also reveals the absence of a gap in the upper anterior toothrow. The occurrence of flehmen in *Felis* (Verberne, 1976) probably provides a method of transporting substances from the upper lip to the nasopalatine canals, circumventing the anterior dentition.

Bovids lack upper anterior teeth altogether; instead, they possess a tough occlusal pad that can act with the lower dentition to crop vegetation. *Ovis* (not figured) has a cleft lip, well-developed vomeronasal organ, and a slight depression in the midline of the anterior palate that may serve as a conduit between the upper lip and the palatine papilla. However, this depression provides a relatively longer and more indirect path between the palatine papilla and upper lip than the median interincisal gap seen in *Eulemur* and *Tupaia*. Estes (1972) described in detail flehmen in ungulates.

Blarina brevicauda has an elongate fold of connective tissue that runs between the central upper incisors, connecting the anterior rostrum and nasopalatine ducts (Fig. 3). Epithelial tissue continuous with that of the palatine papilla surrounds this fold; no lumen is evident within it. Figure 3 shows serial cross sections of the rostrum in *Blarina*, and demonstrates the connections between the paired vomeronasal organ, the nasopalatine ducts, the palatine papilla, and the fold of tissue between the central upper incisors. Certain tenrecine lipotyphlans examined by Hofer (1982) lack this elongate fold of tissue, but are apomorphic in other regards (e.g., in having an unpaired naso-



palatine duct and in lacking a palatine papilla).

Strepsirrhine mammals surveyed here are quite diverse in their rostral morphology (see also Hofer, 1977, 1982). Taxa that are distinct from the pattern seen in *Tupaia* and *Eulemur* include *Felis* (which lacks an interincisal gap), *Ovis* (which possesses a non-dental occlusal pad in lieu of upper anterior teeth), and *Blarina* (which possesses an elongate fold of tissue connecting the upper lip and palatine papilla).

Is the lemuriform and adapiform rostrum autapomorphic?

As documented by Cave (1973) and Hofer (1976, 1977), the most conspicuous rostral autapomorphies among primates are found in anthropoids and tarsiers. With notable exceptions (e.g., *Daubentonia* and lepilemurids including the subfossil *Megaladapis*), significant autapomorphies among strepsirrhine primates are not as well-documented. This is understandable; the rostrum of strepsirrhine primates differs little from that of *Tupaia*, a taxon often used to define primitive states among primates.

However, considerable variability among strepsirrhines is present in the size of the gap between the central upper incisors. Figure 4 shows that in the size of the interincisal gap, most nocturnal lemuriforms, adapids, *Tupaia*, and *Setifer* fall either near or below the mean scaled-gap (by either palatal width or molar area) of all examined taxa. On the other hand, *Eulemur*, *Lemur*, *Haplemur*, *Indri*, and *Avahi*—all of which have been characterized as habitually spending active time with one or more conspecifics—fall well above the group mean. *Phaner* also has a relatively wide gap; interestingly, Charles-Dominique (1978) characterized *Phaner* as more gregarious than other chei-

Fig. 2. Ventral views of rostra in *Eulemur fulvus* (A), *Tupaia minor* (B), and *Felis catus* (C). *Eulemur* and *Tupaia* depend on a gap between the central upper incisors to facilitate communication between the rhinarium and nasopalatine ducts, whereas *Felis* lacks a gap within its anterior toothrow (see text). The palatine papilla is partially dissected in *Eulemur* (A); the lower anterior teeth are intact in *Tupaia* (B) and obscure its palatine papilla; the upper lip in *Felis* (C) has been displaced postmortem. See Figure 1 for abbreviations.

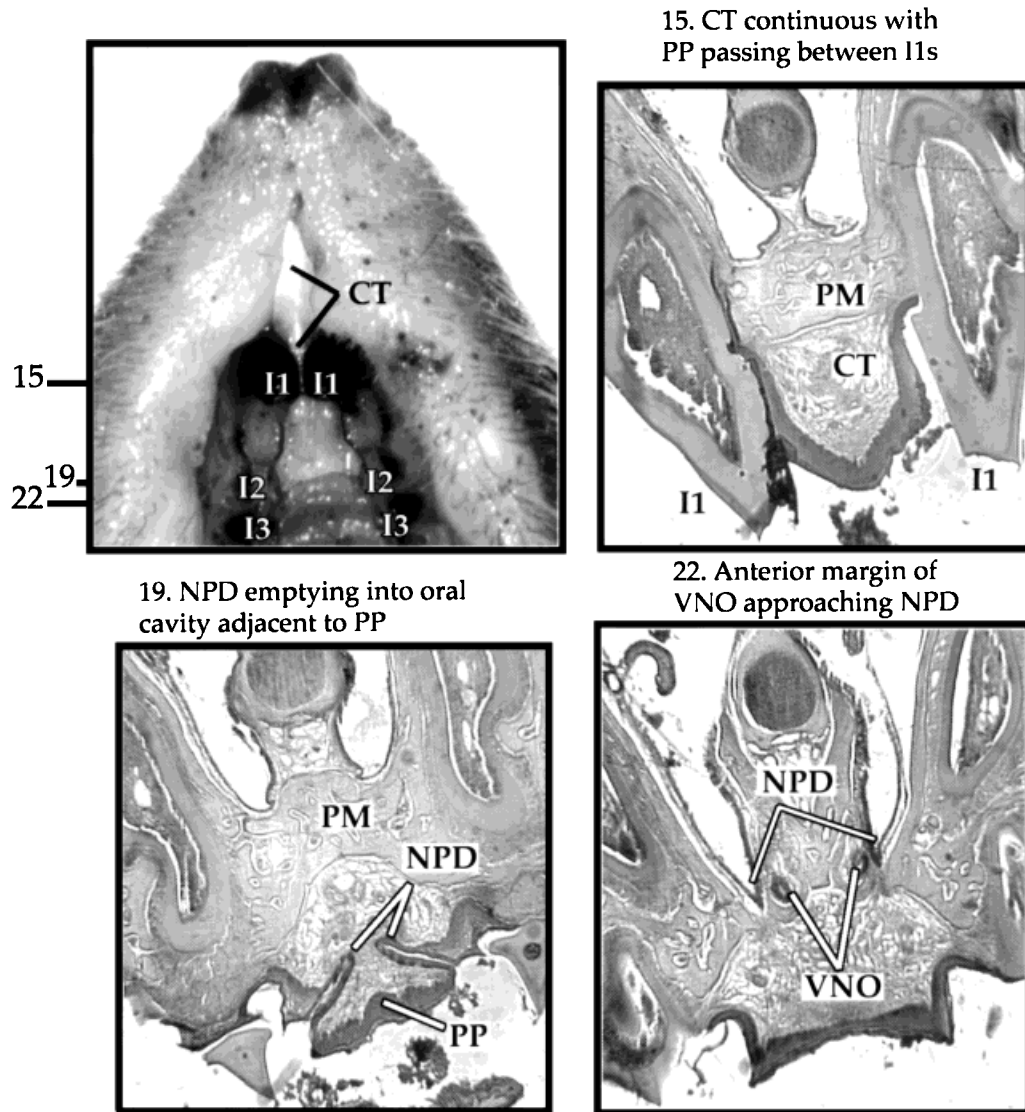


Fig. 3. Ventral view of rostrum (above left) and coronally oriented cross sections of *Blarina brevicauda* (cross sections numbered according to USBA slide). Location of each cross section is indicated in ventral view. Note connective tissue running from anterior rostrum, between central upper incisors, toward nasopalatine ducts. Connective tissue in 15 is surrounded by epithelial tissue continuous with that of palatine papilla, and lacks an internal lumen. See Figure 1 for abbreviations.

rogaleids, and considered its social behavior similar to that of the monogamous small indrid *Avahi*. Animals that do not appear to fit the correlation between gregariousness and wide interincisal gap size are *Propithecus* and *Varecia* (which have relatively small gaps despite being gregarious, although the social habits of *Varecia* are not well docu-

mented). *Euoticus* has an unusually large gap, despite being part of a clade dominated by animals that typically spend active time alone.

DISCUSSION

Returning to the questions asked at the end of the Introduction, it may now be stated

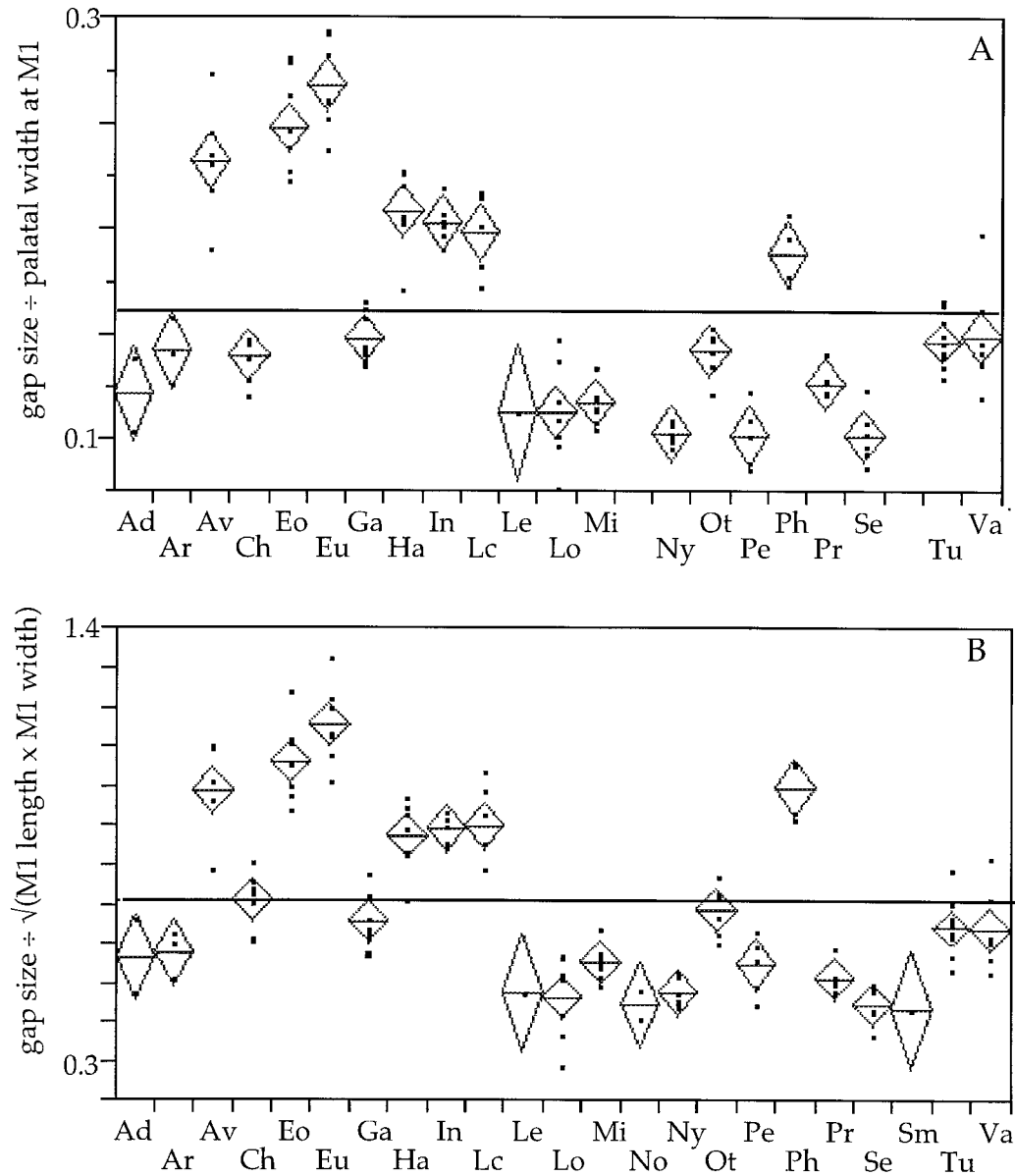


Fig. 4. Gap size scaled by palatal width (A) and area of the upper M1 (B) across strepsirrhine primates, *Tupaia*, and *Setifer*. Dots represent individual specimens measured; diamonds represent 95% confidence intervals of the mean for each taxon; non-overlapping diamonds in any two groups indicate a significant difference at $\alpha \leq 0.05$, assuming normal distribution; horizontal lines represent mean scaled gap size for all sampled taxa. Taxonomic abbreviations (with sample size in parentheses) are as follows: Ad (2) = *Adapis parisiensis*, Ar (3) = *Arctocebus calabarensis*, Av (6) = *Avahi laniger*, Ch (7) = *Cheirogaleus sp.*, Eo (7) =

Euoticus elegantulus, Eu (8) = *Eulemur sp.*, Ga (8) = *Galago senegalensis*, Ha (7) = *Hapalemur griseus*, In (6) = *Indri indri*, Lc (6) = *Lemur catta*, Le (1) = *Leptadapis magnus*, Lo (7) = *Loris tardigradus*, Mi (8) = *Microcebus murinus*, No (2) = *Notharctus sp.*, Ny (6) = *Nycticebus coucang*, Ot (7) = *Otolemur crassicaudatus*, Pe (5) = *Perodicticus potto*, Ph (4) = *Phaner furcifer*, Pr (7) = *Propithecus sp.*, Se (7) = *Setifer setosus*, Sm (1) = *Smilodectes sp.*, Tu (11) = *Tupaia sp.*, Va (7) = *Varecia variegata*. (See Table 1 for individual measurements.)

that 1) no, anatomically strepsirrhine mammals do not display homogeneous rostral morphologies, and 2) yes, data exist that support Rosenberger and Strasser's proposal that some lemuriforms (but not adapiforms) have an autapomorphic rostrum. The implications of each of these answers for the potential link between strepsirrhinism and toothcomb evolution will be explored in turn.

Rostral diversity among strepsirrhine mammals

Outside of primates and tupaiids, the interincisal gap is not a necessary correlate of anatomical strepsirrhinism. This finding is of particular concern to studies seeking to establish the presence/absence of anatomical strepsirrhinism in fossil taxa, which lack information on soft tissue structures. Fortunately, there are other osteological indicators: some lemurs (e.g., *Varecia*) possess bony prongs medial to the central upper incisors that may be related to the tethered condition of the upper lip.

A more consistent indicator may be related to the morphology of the nasal fossa. With the possible exception of some aquatic mammals (e.g., *Phoca*), strepsirrhine mammals appear to be consistently macrosmatic. Across mammals as a whole, a relatively large and complex nasal fossa is better correlated with strepsirrhinism than is the upper interincisal gap. All of the anatomically strepsirrhine animals described here (i.e., *Blarina*, *Eulemur*, *Felis*, *Ovis*, and *Tupaia*) possess a relatively large nasal fossa divided into respiratory and olfactory regions by the posterior transverse lamina (Cave, 1973); however, not all of these taxa possess a relatively large upper interincisal gap. Hence, studies on fossil taxa should incorporate internal nasal osteology in addition to gaps in the anterior dentition to infer the morphology of the soft tissues of the rostrum (e.g., Moorman and Fleagle, 1980).

Gregarious lemuriforms are rostrally autapomorphic

The relatively wide interincisal gap among gregarious lemuriforms is consistent with one of the predictions of the Rosenberger-Strasser hypothesis described above; that is, gregarious lemuriforms have a relatively

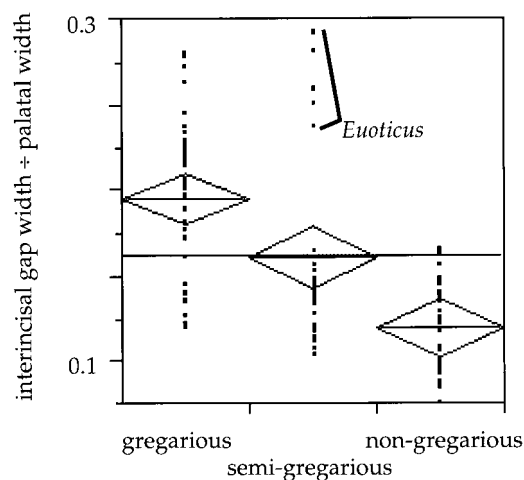


Fig. 5. Interincisal gap width divided by palatal width in gregarious, semi-gregarious, and non-gregarious strepsirrhine mammals listed in Table 1. Diamonds represent 95% confidence intervals of the mean scaled gap width for each group (as in Figure 4). The horizontal line represents the mean scaled gap for all sampled taxa. All "gregarious" points that overlap with the other distributions are individuals of *Propithecus* and *Varecia* (see text).

wider gap between their central upper incisors than other mammals ($P < 0.01$; see Fig. 5). However, the interpretation that this difference is related to function of the vomeronasal organ in frequent allogrooming is admittedly tentative until at least one assumption can be tested by behavioral observations. That is, the complex social structure of gregarious lemuriforms, and the relatively frequent interindividual contact inherent in multi-individual troops and pair-bonds, seem to justify the assumption that gregarious forms spend more time grooming each other than non-gregarious taxa. However, whether or not *Lemur catta* actually spends more time allogrooming than, say, *Otolemur* has not yet been rigorously determined by field observations.

Charles-Dominique (1977) documented that galagonids encounter conspecifics considerably more often than do lorids. In general, the greater level of gregariousness in galagos over lorises is consistent with the hypothesis developed here; galagonids have significantly wider scaled interincisal gaps than do *Perodicticus*, *Loris*, and *Nycticebus*, even when the outlier *Euoticus* (which

greatly increases mean galagonid gap size) is removed ($P < 0.01$; see Fig. 4). The lorid *Arctocebus calabarensis* provides a less-remarkable outlier; the small sample of this taxon examined here does not have a significantly smaller interincisal gap than that of *Galago* or *Otolemur*. There is also considerable overlap between most galagos and tree shrews.

Dietary factors impinging on the morphology of the rostrum are clearly relevant to this study, and may also explain some of the observed variation. The fact that *Propithecus* has well-developed upper anterior incisors and uses them as foraging tools (Szalay and Seligsohn, 1977) is undoubtedly related to the morphology of its rostrum; the same may be said of the anterior dentition in *Varecia*, and in the gummivorous taxa *Phaner* and *Euoticus*. If diet alone is cited to explain the gap size in these taxa, then it does not have a consistent effect, as *Propithecus* and *Varecia* have unusually narrow gaps for indrids and lemurids, and *Phaner* and *Euoticus* have unusually large gaps for cheirogaleids and galagonids (respectively). It is likely that both dietary and social factors had some influence on the morphology of the anterior rostrum in all of these animals; but it is difficult to determine the relative importance of these factors. In any event, more data on the behavior of certain nocturnal prosimians (e.g., *Euoticus* and *Phaner*), and on the extent to which they can be classified as "gregarious," are desirable to test whether the size of the interincisal gap in these animals could be related to frequent grooming.

Despite some exceptions, there remains an intriguing correlation between the width of the upper interincisal gap and social patterns among lemuriforms. Five of seven lemurids and indrids that spend active time with one or more adult conspecifics (*Eulemur*, *Hapalemur*, *Lemur*, *Avahi*, and *Indri*), and one cheirogaleid (*Phaner*) classified as "pre-gregarious" by Charles-Dominique (1978), have significantly wider scaled interincisal gaps than all lorids, cheirogaleids, non-primates, and all but one galagonid. Furthermore, galagonids have significantly wider interincisal gaps than most of their less-gregarious lorid relatives.

If gregarious taxa actually allogroom more frequently than others, then Rosenberger and Strasser's association of anatomical strepsirrhinism with the toothcomb offers at least a partial explanation for their relatively large interincisal gap.

Evolution of the lemuriform toothcomb

This study supports Rosenberger and Strasser's hypothesis that function of the toothcomb is related to anatomical strepsirrhinism. However, it does not support their contention that adapiforms possessed an autapomorphic rostrum.

The shared possession in *Tupaia*, adapiforms, and most non-gregarious lemuriforms of a moderately sized gap between the central upper incisors, tethered upper lip, and palatine papilla (Figs. 3A, 3B) supports the interpretation that this condition among lemuriforms is primitive. This is in accord with Beard's (1988) interpretation that the base of the clade containing adapiforms and lemuriforms was not marked by a reconfiguration of oronasal morphology.

The inference that early strepsirrhine primates had a plesiomorphic rostrum does not necessarily invalidate Rosenberger and Strasser's conclusion that the adapiform rostrum was "preadaptive" to the lemuriform toothcomb. Primitive characters can, after all, have functional importance and at the same time be integrated with a novel functional regime (e.g., phalangeal curvature in early hominids; see Susman et al., 1984). However, without some sort of decisive anatomical evidence, it is difficult to test when and how the adapiform rostrum became "preadaptive," and decide which similarly configured non-primate rostra are not "preadaptive."

It is therefore unclear that allogrooming as a means of collecting pheromones was the phylogenetically primary function of the lemuriform toothcomb. Taxa that possess relatively wide gaps—argued here to be associated with grooming—appear to be well-nested within the Strepsirrhini (Fleagle, 1988; Yoder, 1996); hence, I tentatively regard diet-based hypotheses of toothcomb origins (e.g., Martin, 1972; Rose et al., 1981) as plausible explanations.

Finally, interesting—but anecdotal—information on dental combs in nonprimates is worth reviewing at this point. To my knowledge, the only other mammal with a well-developed dental comb known to be used for allogrooming is the dermopteran *Cynocephalus* (Aimi and Inagaki, 1988). This taxon is interesting because it possesses a very wide diastema in the upper anterior toothrow. The behavior of *Cynocephalus* in the wild is poorly known (see Lekagul and McNeely, 1977; Lim, 1967; Wharton, 1950). However, the evidence presented here can be used to make a prediction: i.e., colugos are social and, as in lemurids, allogrooming occurs with relative frequency and plays a socially significant role. The wide interincisal gap in colugos results from the need for a wide path from the anterior rostrum to the vomeronasal organ in a taxon that allogrooms, collects conspecific pheromones, and uses its vomeronasal organ to process them. Hopefully, sufficient behavioral data on living dermopterans will someday be collected to test this hypothesis.

CONCLUSIONS

The gap between the central upper incisors characteristic of lemuriform primates and *Tupaia* is one of several ways in which contact between the vomeronasal organ and rhinarium can be established. Other mammals have evolved specialized means involving morphology (e.g., the elongate fold of connective tissue in some lipotyphlans; see Fig. 3) and behavior (e.g., flehmen in bovids) for this purpose.

Among strepsirrhine primates, gregarious lemuriforms have apomorphically large gaps between their central upper incisors (Fig. 5). This observation is consistent with the functional link between anatomical strepsirrhinism and dental grooming proposed by Rosenberger and Strasser (1985). However, adapiforms and non-gregarious lemuriforms do not appear to share significant rostral apomorphies. It is therefore difficult to infer the extent to which social factors influenced the origin of the toothcomb in early toothcomb prosimians.

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